Camouflage in a dynamic world

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Abstract
We review how animals conceal themselves in the face of the need to move, and how this is modulated by the dynamic components and rapidly varying illumination of natural backgrounds. We do so in a framework of minimising the viewer's signal-to-noise ratio. Motion can match that of the observer such that there is no relative motion cue, or mimic that of background objects (e.g. swaying leaves). For group-living animals, matched motion and coloration is a special case of the latter 'motion masquerade', where each animal is a potential signal against the noise of other individuals. Recent research shows that dynamic illumination, such as underwater caustics or dappled forest shade, greatly impedes detection of moving targets, so may change the balance of predator-prey interactions.

Introduction

The study of coloration in the natural world provides a common focus for vision scientists, evolutionary biologists, animal behaviourists, ecologists, geneticists and optical physicists [1]. The understanding of camouflage, for example, has seen great advances through this interdisciplinarity, and recently there has been a surge of interest in the interaction between coloration and behaviour, particularly movement [2]. Motion is the enemy of camouflage, because the common fate of moving features creates pop-out of figure from ground [3,4*] and can aid in object identification [5]. However, most natural scenes themselves contain dynamic elements – motion of objects in the background, such as vegetation, and rapid variation in the illumination. So, segmentation of a moving target, and discrimination from distractors, may not be as straightforward as in the psychophysics lab. In this review, we examine the extent to which the principles that explain the varied mechanisms of static camouflage in a static world apply in a dynamic visual environment. We discuss recent research on the extent to which dynamic illuminants and dynamic backgrounds relax the constraints on movement by camouflaged animals, and how behaviour can reduce the probability of detection and identification.

Camouflage is achieved through multiple mechanisms, and different valid taxonomies exist [6], but a useful framework for the current review is minimisation of the signal-to-noise (SNR) ratio [7]. The signal can be the whole organism and its attributes (identity, edibility, likelihood of capture, etc.) or lower-level features (surface luminance, colour

or texture; edges) that might lead to detection and subsequent identification (Table 1 in [7]). Some camouflage strategies work by reducing the signal (e.g. background matching), some enhance noise through false identity cues, some do both (e.g. disruptive coloration) [7].

Engineers and computer scientists are showing increasing interest in how to reduce the detectability of motion, particularly in the context of autonomous vehicles, and many of the proposed solutions are biologically inspired [8,9*]. We review such examples of motion camouflage, but extend this to avoiding detection within a world that is itself dynamic.

A dynamic world

Motion is ubiquitous in natural environments, varying in source, form and relevance, and animals have a range of neural mechanisms to deal with different tasks in which motion is relevant: simple object tracking, rapid detection of looming stimuli that might represent approaching threat or risk of collision, flow-field analysis from self-motion to guide movement, motion parallax for depth judgement [10]. Some dynamic features of a scene may be considered to be moving randomly (at a given spatial scale – e.g. moving leaves on a tree viewed from a distance), while some will consist of local coherent directed motion (e.g. a moving leaf on a tree viewed close-up, tumbleweed passing, directed caustics from water flow, passing shadows of overhead objects in air or water). Detecting a relevant moving object will therefore involve detection of non-random motion of features and perceptual binding into a 'target' (a dynamic signal), and its discrimination from irrelevant moving objects (dynamic noise).

The motion of objects within the environment is the most common source of non-random dynamic noise. For example, physical features (e.g. vegetation, substrate, debris, or the water's surface) moved by wind, by water currents or tidally. An additional case of background motion is that of other organisms, particularly those that move collectively within a habitat. The distribution of velocities will be dependent upon the social ecology of the organisms involved. For example, European starlings, *Sturnus vulgaris,* form highly coordinated flocks [11], while a swarm of *Daphnia* would represent something closer to (but not actually) random movement [12]. For a group-

living animal, conspecifics become the background from which, in the case of a predator attack, it is important not to be readily individuated [13].

In bright conditions, a common biproduct of dynamic physical features within the light-path is the resulting variation of local illumination [14]. Varying illumination also introduces dynamic noise, which varies in time and space, and is prevalent in both the terrestrial (e.g. dappled light) and aquatic (e.g. water caustics) domain (Figure 1). Dappled light is a consequence of light passing through moving foliage [14], while water caustics are created by the diffraction and convergence of light through a spatially heterogenous water surface [15,16]. The form of both dappled light and caustics is a function of the forces acting on the given physical feature (vegetation or waves), including the strength and direction of wind, the altitude and angle of the sun, and the depth/height between feature and substrate [14,16]. Though both are common in their given domains, they differ in their scope: water caustics are more global in their influence than dappled light, which is often localised at the margins of shade [14]. Indeed, the presence of these illuminants within particular habitats has been closely linked to some aspects of concealment. The vertical barring and vermiculation of fish [16] and some felid coats [17] have been considered adaptations to the (static) consequences of such illumination. More fundamentally, water caustics could also have played a significant role in the initial evolution of colour vision [18]. With spatio-temporal noise induced by variable illumination, the ratio of stimulation of photoreceptors tuned to different wavelengths is more stable than the average light intensity signal, so a more reliable cue to where one object ends and another begins [18].

One potential source of dynamic information is self-induced. Many organisms do not view natural scenes entirely from a fixed position but do so on the move. When an organism moves, objects within the viewed scene (irrespective of their relevance and motion) will elicit apparent motion across the organism’s retina, termed optic flow. Differences in optic flow, because of differences in the correlation of apparent motion of objects in different depth planes, can be used to break camouflage, with or without stereopsis [19,20].

It is within the context of such motion – of background objects, of light, of other organisms – that an animal must conceal itself, whether to avoid detection or recognition by predators, or to surprise its own prey. We now consider strategies which, following the framework of Merilaita et al. [7], either minimise the signal or enhance noise.

Minimising the signal

Background matching in the temporal domain includes self-motion that is similar to that of a dynamic background, and slow motion that is undetectable against a relatively static background. The most commonly proposed example of the former is the swaying motion of a stick insect (Phasmidae) with the movement of plants in a light breeze [21]. However, the behaviour is also consistent with the animal maintaining balance and contact with the substrate [2,22]. More convincing is Fleishman's [23] analysis of the neotropical vine snake *Oxybelis aeneus* that, when stalking prey, shows sinusoidal oscillations at the same frequency as the surrounding wind-blown foliage, while Ryerson [24] identifies three species of colubrid snake that pair head oscillations with a dorsal pattern to achieve the same result. Again, these examples may be better classed as motion masquerade, false signals of identity (increased noise) rather than inconspicuousness through background motion matching. In fact, unequivocal evidence for the latter is sparse, the reverse problem having attracted more empirical research: how dynamic signals are designed to stand out from dynamic background noise; e.g.[25]. That said, the theoretical framework and computational tools developed for the latter are ideal for analysing motion camouflage itself [26-28*].

Primates are acutely sensitive to motion of even low contrast targets, detecting them rapidly in advance of recognition [29], and characteristic coherent motion of even a small number of features can be used in identification by humans and other animals, the basis of 'point light' or 'biological motion' experiments [30]. Therefore, moving slowly and/or in a saltatory fashion is an obvious way to minimise a motion signal against a relatively static background. The stalking behaviour of predators such as cats exemplifies this but, surprisingly, this has never been related, quantitatively, to the motion detection thresholds of relevant prey. Minimisation of motion signals may be why cuttlefish, which are capable of rapid colour change [31], switch to low

contrast patterns when moving [32]. They also change their mean whole-body reflectance as they move over light or dark substrates [33], but only if the patch size is larger than their body length [34]; again consistent with reducing a motion signal (Figure 2).

The best characterised example of a behaviour designed to minimise the motion signal is the tracking flight of territorial (or mate-chasing) insects. In hoverflies [35] and dragonflies [36], a pursuer matches its relative position and speed to that of the target individual such that its projected image on the target's retina is relatively invariant, and so the optic flow is similar to that created by the background. The algorithms that an insect might use to achieve this have, more recently, been applied to control systems for missiles and ships that seek to intercept a target whilst minimising their own detectability [8,37,38] (Figure 3).

In the situation where the background motion signals are due to other organisms, and they are similar to the target in form and motion – e.g. a flock of birds or shoal of fish -- they act as 'distractors' to the 'target'. Here target-distractor similarity in appearance impedes individuation and target tracking [3,13,39], as does similarity of motion [40].

Increasing the noise

If it is not possible to reduce a motion signal, the alternative for increasing SNR is to seek environments with high motion noise [7]. Would this work? Matchette et al. [27*] used computer-simulated scenes to investigate how prey detection was affected by the presence of water caustics and dappled light. When asked to capture moving prey items, human participants were significantly slower and more error-prone when viewing scenes with illumination that was dynamic as opposed to static. Whether this holds for wild animals is yet to be tested. If true, one would predict some level of habitat selection: mobile prey should seek safety in environments with moving background elements and/or illumination, while visually-orientated predators should hunt preferentially in low-dynamic-noise environments.

Motion is typically coherent and directed, and consequently predictable. While irrelevant motion of the environment may provide a temporary blanket of visual noise,

with which to mask overall detection, there are means by which an organism itself can lessen the coherence and predictability of a motion signal. A long-proposed solution is protean motion: movement that is sufficiently unpredictable so to minimise a predator's ability to anticipate future position or action [41*]. Although untested, protean movement could even act as a moving equivalent of disruptive colouration, by reducing the viewer's ability to bind features into a single percept, in this case by coherent motion. Iridescence, where the hue and intensity of the reflected light varies with the angle of view and illumination, impedes object recognition [42] and so, along with other mechanisms of rapid colour change [43], could have similar effects.

The coherence of motion can also be broken by punctuated motion, achieved by bouts of movement (regular or irregular) or movement obscured via occlusion by the habitat. In both cases, the viewer is forced to estimate the direction and speed in order to extrapolate the next position. False cues of direction or speed can introduce error via so-called dazzle coloration [39,40,44-47]. Here, high contrast, repetitive patterns induce contradictory or biased motion cues [48], influencing estimations of speed [46,49] and/or direction [44]. Interference with optic flow cues may be why biting flies are deterred from landing on zebras [50]. Speed judgement errors can be accentuated by internal pattern motion in addition to whole-body motion [49,51], much like the 'passing cloud' display of cuttlefish [31].

The role of attention

Attention – a central concept in psychology – can be characterised as the process of selectively focussing on one thing whilst ignoring others [52]. Crucially, attention is a limited resource, and this has important implications for the detection and identification of moving targets. In terms of a SNR framework [7], attention can be thought of as increasing the signal, decreasing the noise, or both. In the context of motion and concealment, attention has a critical role: it allows what might otherwise remain undetected (or unidentified) to be revealed; conversely, a lack of attention, or an inability to attend to a specific target, will potentially afford that target protection. The success of slow movement for avoiding detection lies more in escaping the attraction of attention rather than sub-detection-threshold motion *per se* [53].

An example of the enhancement of the visibility of a stimulus is attention guiding eye, head and body movements in order to place the target within the visual field of the high-acuity fovea. However, attention is more than optimising sensory input; it is enhanced neural processing and so can occur covertly without a shift in gaze [52]. Thus, attention can alter apparent spatial resolution [54], perceived perceptual organisation [55], the stability of fixations [56], and be moved predictively to where a moving target is likely to be [57]. However, the fact that attention is limited can be exploited by prey via the confusion effect: the reduced predation success caused by difficulty in individuating prey items in a group [58]. This inability to pick out a single item can be attributed to an attentional bottleneck in the cognitive system of a predator. Increasing numbers of similar-looking, potential prey items make the targeting of a specific individual more difficult because of the expanding attentional resources required to separate the target from distractors. Coloration [39], density [11,58] and behaviour [40] influence the magnitude of the effect.

Conclusion

Motion camouflage may sound like an oxymoron given that, perhaps more than any other cue, movement breaks camouflage. However, evolution has equipped animals with strategies to conceal or ambiguate motion signals, and research in this field is accelerating. New hardware and computational tools are facilitating the characterisation of dynamic visual information in natural environments, and that available to animals moving through them. Combined with psychophysical and behavioural measures of detection and recognition performance, we are starting to understand how behaviour and coloration can be combined to minimise detectability in a dynamic world. However, it is attention rather than sensory constraints which will often limit the detection of camouflaged targets, even when they move. The next breakthrough is therefore likely to come with a better understanding of attentional processes in non-human animals and how attention is deployed when moving through natural, dynamic, environments.

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Conflict of interest

The authors declare no conflict of interest.

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Using animations of camouflaged, walking, human figures, the study found that detectability was not a simple function of the speed of the target, but that this interacted with both local contrast and spatial frequency match to the background. Motion breaks camouflage but even at fast movement speeds, low contrast reduces detectability, echoing results from cuttlefish (Figure 2).

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Pursuit trajectories of flying insects intercepting targets (prey, territory intruders or potential mates) are a classic example of motion camouflage; the flight path is such that the image on the retina of the pursuee stays constant [10,11]. The authors of this new paper implement an algorithm that achieves this, subject to realistic flight constraints, in an unmanned aerial vehicle.

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The authors show that natural iluumination dynamics, both dappled forest shade and underwater caustics, significantly reduce subjects' ability to detect moving targets. So, while motion breaks camouflage, the costs are substantially reduced in such habitats.

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This is an excellent paper for biologists interested in how to quantify motion in natural backgrounds (vegetation swaying in the wind, etc.) and to examine the match (camouflage) or strategic mismatch (signals) to that background. The authors analyse the dynamics of the backgrounds against which two populations of Australian lizard display, and provide suggestive evidence that their behaviour has diverged in response to differences in those dynamics.

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If you can't evade detection, move in such a way to make interception and capture difficult. This paper tests the effect of unpredictable ('protean') movement on capture success of moving targets, and does so in a virtual reality setting. The study therefore showcases a powerful research paradigm as well as the long-assumed, but rarely tested, effects of protean behaviour as a defence.

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Figures

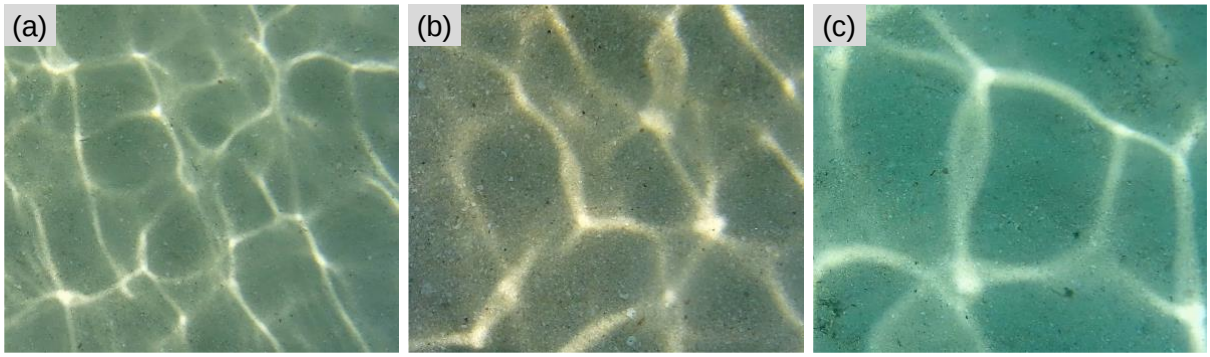

Figure 1: Screenshots of water caustics on a sandy seabed at (a) 0.5 m, (b) 1.0 m and (c) 1.5 m (Lizard Island, Great Barrier Reef, Australia: 14°40 8 S, 145°27 34 E). All were filmed at midday under calm conditions using an Akaso V50 Pro (Akaso, www.akaso.org) positioned 40 cm above the substrate.

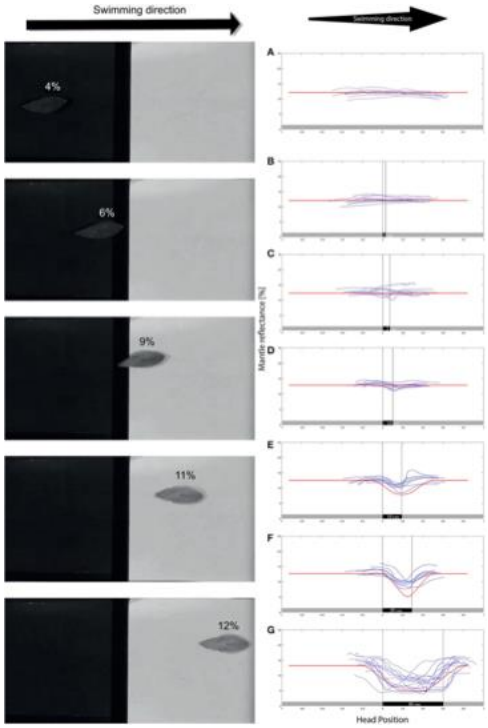

Figure 2: Left: video frames from film of a European cuttlefish swimming over dark and light substrates (reproduced with permission from Josef et al. 2015). Right: reflectance from the mantle of eight cuttlefish (blue lines) swimming over dark substrate of varying widths, and the outcome of a computer model based on the animal's field of view (red lines). Animals only adjust their colour if the patch size is larger than, approximately, their body length. Reproduced with permission from Josef et al. (2017).

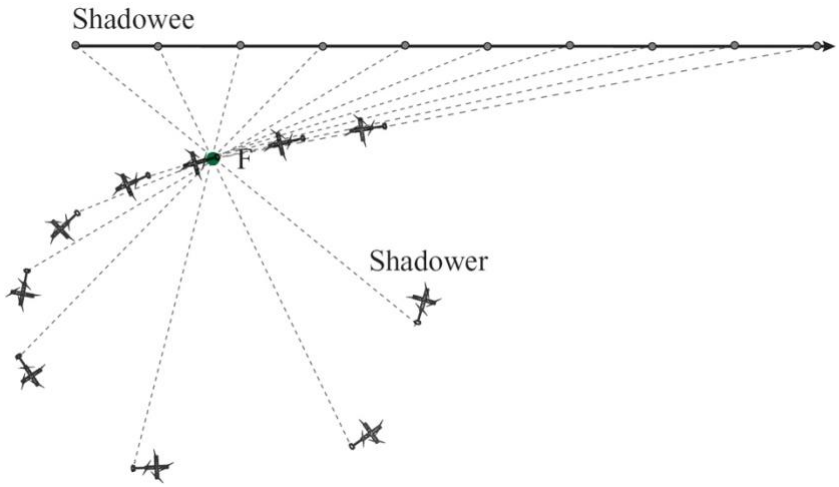

Figure 3. Simulated path of an unmanned aerial vehicle (the ‘shadower’) tracking a target (the shadowee’) while implementing a “constant distance motion camouflage” algorithm. The latter is thought to be analogous to that used by aerial insects pursuing flying prey whilst minimising their own detectability. The algorithm is such that the shadower is perceived as a stationary object by the shadowee while maintaining a constant distance. In Strydom & Srinivasan’s implantation additional realistic constraints were included regarding the vehicle’s flight capabilities in terms of speed and acceleration. Reproduced with permission from Strydom & Srinivasan (2017).

Graphical abstract

Visual search in a dynamic world: a predator’s view of a school of fish. The average motion signal of the target (purple arrow) has to be discriminated from the motion noise (orange arrows) of the illuminant, background, other animals and, for group-living species, conspecifics. The target itself may produce dynamic motion noise via coloration (pigment patterns and/or silvered/iridescent scales) and behaviour.